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ROUND SHAPE COMBS PRODUCED BY STIGMERGIC SCRIPTS IN SOCIAL WASP

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Abstract

In this paper we look for simple building scripts, which are able to produce similar round shape combs, which commonly can be found in the nature. Distinct stigmergic algorithms (namely: ideal, optimal, random and differential) are presented, which based on different rules and conditions, but produced forms, which are sufficient from an ecological and economical point of view (round-shaped combs). The analysis of the natural nests and our observations on the building behaviour of the wasps lead us to study how the simple behaviour rules, which have definite random components, are able to create a complex nest only through the accumulation of material.

In these stigmergic algorithms the wasps meet only the local configuration. This determines the behaviour of the builder, which in the present study was reduced to initiate a new cell on the circumference of the comb. The growing process was the result of the individual wasps following simple behavioural rules based on local cues. During the construction the wasps modify their environment providing new stimuli, which induce new behavioural responses, which in their turn modify the environment. The combs emerge from this dynamic stimulus-reaction. Indirect communication between the wasps through the construction can lead to the formation of complex and regular nests in the absence of any plan either centralized or in the heads of each individual.

Both natural and simulated nests developed in a fashion matching a power function. The dynamics of "differential script" did not differ significantly from the natural building in the natural range of this species.

1. Introduction

The nests of social insects provides an interesting enigma because the architectural complexity contrasts with the builders' limited intelligence. The structure is coherent and it is usually much larger than the individual builder (Hansell, 1984).

From the point of view of behavioural ecology, wasp nests present fine examples of adaptation to selection pressures on economy and colony defense (Jeanne,1975; Ogushi et al., 1990). In contrasts to these well known aspects, questions how wasps build their nests have been neglected. There are some detailed experiments on building (e.g. Gervet, 1966; Downing and Jeanne, 1988, 1990) or detailed analyses of nests (e.g. Downing and Jeanne, 1986, Wenzel, 1991, 1992), but we only poorly understand the mechanisms by which a group of wasps constructs a complex nest form.

To varying degrees, the wasp societies are composed of one to several thousand individuals, characterized by the simplicity of their behavioural repertoire, their limited individuality and the inherent randomness in their behaviour. The structures built by these groups appear highly deterministic, so it is not suprising that a blueprint has been thought to be explicitly possessed by the individual. Theoretical studies (Theraulaz and Deneubourg, 1992; Karsai and Pénzes, 1993) show that this is not necessarily the case. Indirect communication between the wasps through the construction can lead to the formation of complex and regular nests in the absence of any plan either centralized or in the heads of each individual.

Although Grassé (1959) and Wilson (1971) decades ago directed our attention to the importance of the "reconstruction of mass behavior" from the individual decision and behaviour, it has recently become apparent, that the principles of self-organization are crucial to understand the functioning of insect societies (see as overview Franks 1987; Deneubourg and Goss, 1989; Camazine, 1991). In this manner the wasp colony can be defined as a set of mobile units. This group is characterized by the collective resolution of the problem (Theraulaz et al. 1991) (i.e. building behaviour). In these systems complex behaviours can be observed and can result in complex patterns (i.e. nest of the colony), even though the constituent individual behaviours are very simple and have strong random components. Local information and constraints control the behaviour of each individual. No direct interactions are necessary to coordinate the work of the group, but the interactions between the nest and wasps are enough for this. During the construction the wasps modify their environment providing new stimuli, which induce new behavioural responses, which in their turn modify the environment. The combs emerge from this dynamic stimulus-reaction.

In a two dimensional system our goal is to seek simple stigmergic scripts, which produce round-shaped combs similar to those found in the nature. The combs built by these algorithms will be compared with each other and the real nests based on the circumference and the eccentricity of the combs.

2. The structure of the comb

Consider a comb structure composed of rings (R) of perfect hexagonal cells (N), with an initial cellular core (black cells in Fig. 1). The comb development is the consecutive addition of cells to the previously constructed structure. Every new cell is built to the circumference of the comb, which consists of S walls. The shape and the compactness of the comb in our two dimensional systems can be rendered by the number of outer walls (S) at a given cell number. The values of S and N can be calculated easily in the case of simulated structures and can be measured in the natural nests as well. At the beginning of the nest development, the number of outer walls (S) larger than the number of cells (N). Because N increases with as the square of ring number and S incrises linearly, cell number exceeds the outer wall number when the comb consists of 48 cells. Since both the numbers of cells and the outer walls are a function of ring number, we can describe the S as a function of cell number (in case of closed rings):

$$S(N) = 2 * \sqrt{3} * \sqrt{(4N - 1)} \qquad (1)$$

In the next section we describe some simple stigmergic scripts, which are able to produce approximately round shaped combs, which can be found frequently in several wasp species. In our two dimension systems one cell initiation happens at every time unit.

3. Building scripts

3.1. The "ideal" building

We defined the "ideal" building as a starting point, which is easily derived and serves as an important reference for comparing different scripts. Ideal building is deterministic: the wasps built every new cell next to the previous one in the same ring. The wasps begin a new circle only after the previous ring is completed. In this way the circumference of the comb is the smallest (comparing the others scripts at the same cell number) and the comb is centered. The numbers of outer walls are a step-wise function of the total number of cells (Fig. 2). There were six steps between two consecutive states, when the rings were perfectly completed in the comb. When a circle was completed the number of outer walls could be described with (1).

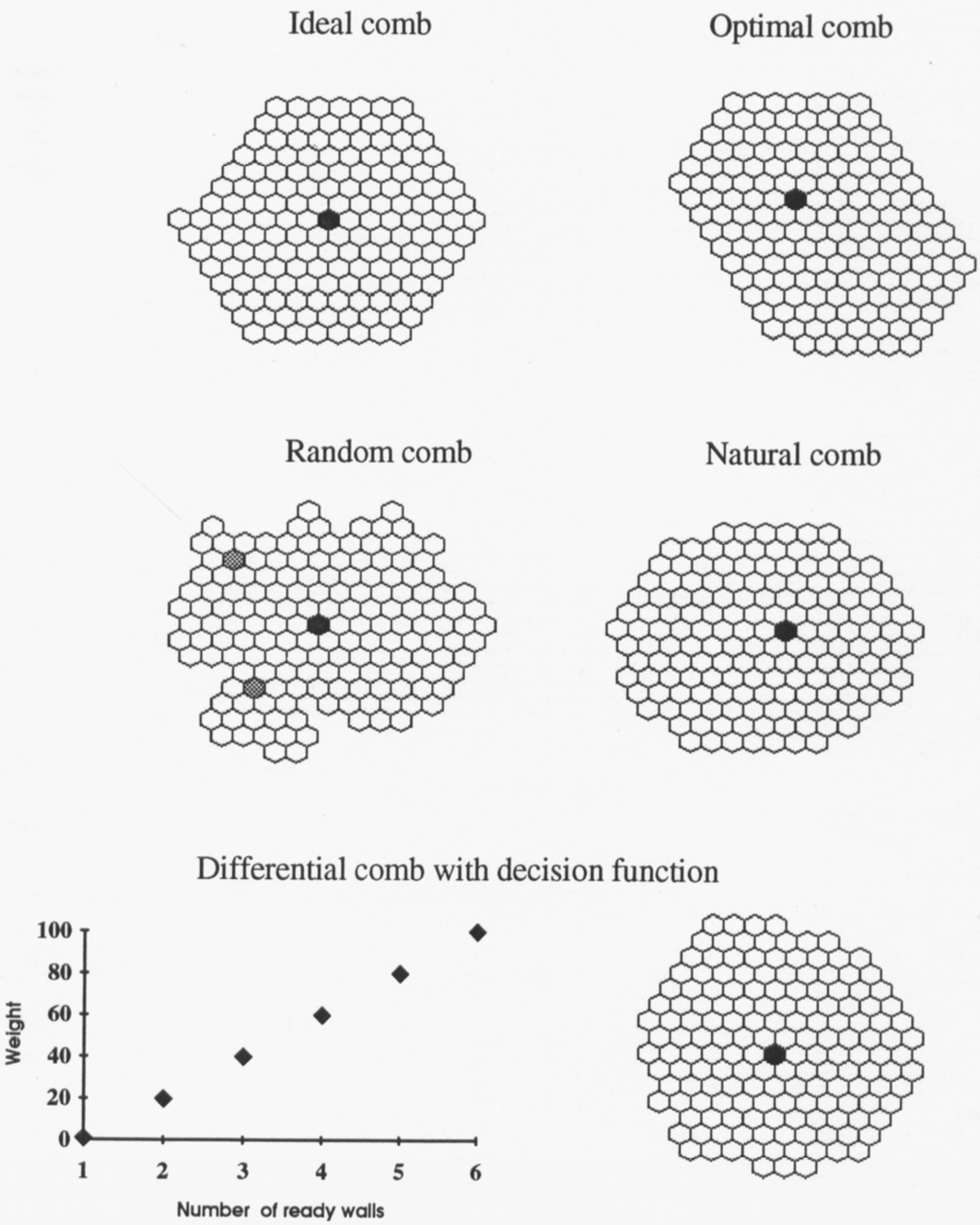

Fig. 1. Combs built by different scripts and the 'natural' wasps (N = 161). Black cell: first cell; gray cells in the random script: holes (bottomless cells) in the structure.

3.2. The random script

The ideal script is very deterministic, the wasp always builds the new cell next to the previous one. As an other utmost point can be conceived the random building, when the wasp initiates the new cell independently from the previous initiation. It means, the wasps initiate new cell anywhere on the circumference of the comb, where at least two ready walls are present for this new cell (the governing role of the two adjacent cells in the building was proved by Downing and Jeanne, 1990). As the comb grows, protuberance-like small irregularities on the circumference of the comb frequently occur (Fig. 2). These structures disappear sooner or later, because they provide relatively large surface for the initiation and their bases became wider and wider or they fuse with the adjacent protuberance. In the meantime new irregularities emerge somewhere on the circumference of the comb.

The other exclusive property of the random script is the temporal occurrence of holes in the comb. These holes consist of cells (most frequently only one cell), which has no bottom and they emerge simply because all of their neighbours are built. These holes occur at the periphery of the comb, but eventually the script fills them in and they disappear, thus these holes rather take place in the periphery region of the comb.

3.3. "Optimal" building

The "optimal" building script determines the placement of the new cell by adding a new wall to the most developed, but still incomplete, region. The script called "optimal" because it places material at the location where it will have the most immediate benefit, where it is most likely to produce a complete cell. If there are several regions of equal development, the choice among these is random. In this manner the optimal building not so deterministic as the ideal one. Although the behaviour of wasps building in an ideal way differ from the optimal ones, in both script the builders initiate the new cell where the most ready walls are ready for the initiation (optimal material usage). For example, when there ae two ready walls for every potential new cells around the circumference, then the choice for the builder is the same whether it initiates a new cell in an incomplete ring or the first cell of a new ring. After this decision the building can be more deterministic for a short time depending on the stimuli, which come from the structure: If one potential new cell occurs with three ready walls in the case mentioned above, the next cell will be built always near this cell until the three-walls situation is exist.

3.4. Differential script

In the previous scripts the decisions of builders are coarse. The wasp looks for a peculiar site (next to the previously initiated cell in the same ring (ideal), or the more complete potential cell (optimal)) to initiate a new cell. In the temporal absence of these specific conditions (i.e. complete rings in the case of ideal and having only two walls of every potential new cell in the case of optimal building) the builder decides randomly about the site of initiation. In the case of these two scripts after the occasionally random decision the further building becomes very deterministic again for a period of time. In the case of random building the builder's decision is always random, because no specific decision is defined.

The differential script avoids both the fluctuations between the random and deterministic decision and the insensitivity of the random script to the previously constructed structure. In differential building, every potential new cell has a chance to be initiated at any time. This chance is not equal, unlike the case of the random script, but it is the function of the ready wall number of potential new cells. (Fig 1.). In this way all potential cells with a definite moment compete with each other simultaneously to be completed.

4. Comparing combs built by different scripts

Fifty parallel simulations were performed for every script mentioned above. The number of outer walls and the eccentricity were calculated at every comb size (in terms of cells). The curves represent the average value of the number of outer walls (Fig. 2) and the eccentricity (Fig. 3) at a given comb size.

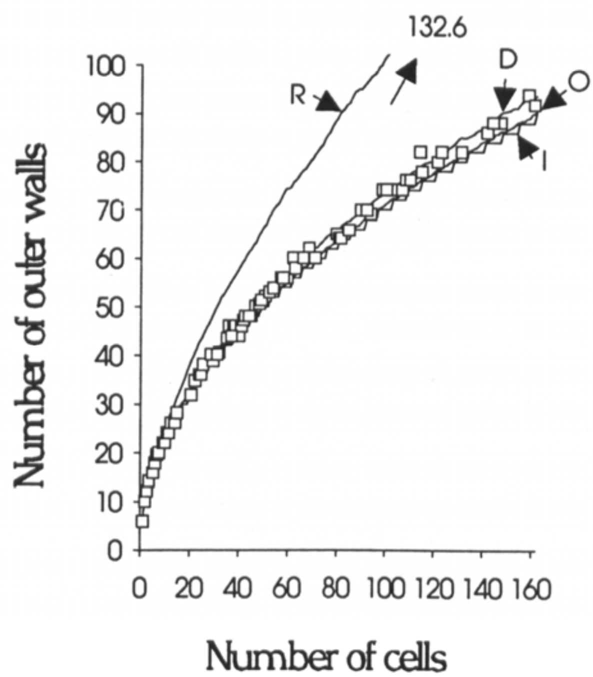

Fig. 2. The average number of outer walls as a function of the cell number. Scripts: I: ideal; O: optimal; D: differential; R: random script. Marker: □: average values of natural nests.

None of the presented stigmergic scripts were able to produce as compact structure as the ideal one (Fig. 2).The compactness of optimal combs was a little bit less than the ideal one, and due to the temporal random initiation the average curve never showed step-wise function. These two were common properties with the random and the differential scripts as well, but they diverged more definitely from the ideal combs than the optimal ones. The increased role of randomness in building produced less compact structure.

One hundred and fifty nests of *Polistes dominulus* Christ were collected and analyzed to compare the structures built by wasps and the stigmergic algorithm mentioned above. The range of nest size was from 1 to 161 cells. When more than one nest belonged to the same size (in terms of cells, as the simulated ones) the average measurements (e.g. average number of outer walls) were calculated. In this manner we obtained 71 different sized nests.

Any kind of building scripts produced more or less similar comb development dynamics (Fig. 2). The average curves, similar to those, which is described by (1): they seemed to increase as a power function of the number of cell. To estimate the curve function, regression analyses were carried out after logarithmic transformation, . We used the following power function for both simulated structures and natural nests:

$$S(N) = a * (4N - 1)^b \qquad (2)$$

where ln(**a**) was the constant and **b** was the coefficient of the linearized form of (2).

All of the fits showed very high coefficient of determination (R squared Table 1). Both parameters of all regressions were tested and compared (t test). In all cases the parameters were significantly different from each other ($p < 0.05$), except three cases (Table 2). The dynamics of ideal script did not differ significantly from the optimal (Coefficient) building dynamics, perhaps due to the similar optimal material usage. The dynamics of differential script did not show significant difference with the natural wasp construction. Both parameters (Coefficient and Constant) supported this insignificant difference.

Table 1. Regression parameters of the linearized function of the outer walls and number of cells (2) in the case of different script and natural nest.

Script type	N	Coefficient (Std.Err.)	Constant (Std.Err.)	R squared
Ideal	161	0.491 (1.066E-3)	1.308 (5.929E-3)	0.9993
Optimal	8050	0.490 (2.290E-3)	1.330 (1.274E-3)	0.9982
Random	8050	0.593 (8.877E-4)	1.052 (4.939E-3)	0.9823
Differential	8050	0.503 (2.950E-4)	1.288 (1.641E-3)	0.9972
Natural	72	0.502 (2.245E-3)	1.283 (1.155E-3)	0.9986

Table 2. Comparing the regression parameters of different scripts and the natural building. Coeff: significant regression coefficients; Const: significant regression constants; NS: non significant parameters (t test $p < 0.05$).

	Optimal	Random	Differential	Natural
Ideal	Coeff	NS	NS	Const
Optimal		NS	NS	NS
Random			NS	NS
Differential				Coeff Const

The first cell was used as the reference point to measure the eccentricity of the combs. Due to the properties of the ideal script, the structures built in this way remained radially symmetrical. The combs built by the other scripts or wasps became more or less off-centered (Fig. 3). The differential script produced the less eccentric combs in this range. The optimal and the random script produced more eccentric combs as the previous script, but even these structures remained well centered comparing the possible maximum value (this is 7 in case of an ideal comb of 161 cells). Generally the natural nest also possessed similar moderate eccentricity.

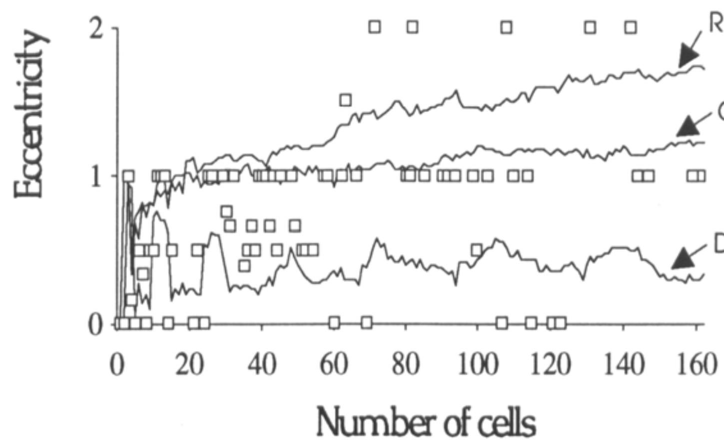

Fig. 3 The average eccentricity of the combs as function of the cell number. Scripts: O: optimal; D: differential; R: random script; □: average values of natural nest.

5. Discussion

In this paper we looked for simple building scripts, which are able to produce similar round shape combs, which commonly can be found in the nature (Wenzel, 1991). Theraulaz and Deneuboug (1992) reveal the important difference between the sequential and stigmergic building algorithms. Our aim was to present distinct stigmergic algorithms, which are very different, but the builders with these simple rules were able to solve their "building problems" and construct nest forms, which are sufficient from an ecological and economical point of view (Jeanne, 1975).

In these stigmergic algorithms the wasps meet only the local configuration. This determines the behaviour of the builder, which in the present study was reduced to initiate a new cell on the circumference of the comb. The growing process was the result of the individual wasps following simple behavioural rules based on local cues. The ideal building was very deterministic, the wasps building in this way had only one possibility: they built next to the previously initiated cell. Although it is easy to depict correctly the results of this behaviour, there is no biological evidence, which clearly supports this script.

The analysis of the natural nests and our observations on the building behaviour of the wasps lead us to study how the simple behaviour rules, which have definite random components, are able to create a complex nest only through the accumulation of material. In the optimal building, the wasp looked for the potential new cell, which initiation would be the most economic locally. When more competent sites were found, the wasps decided randomly among them. The comparisons of these structures to the real nest illustrate quite clearly that the optimal building is not the most appropriate script to understand the natural building behaviour. This script also deterministic and the temporal random choices have great effects to the further building.

Bees and ants do not assemble and use mental topographic maps when they forage (Wehner and Menzel, 1990). It is reasonable to assume that the wasps do not search for the previously constructed cell or the most economic initiation site on the comb, rather respond with distinct sensitivity to the local situations. The differential script simulated this situation. This script results in very similar architectures, which are built by the natural wasps.

The increased role of randomness in the script produced less compact structure. The wasps building by random script were insensitive with respect to the previously constructed structure. Although these combs remained more or less centered and round-shaped, temporal faults and irregularities occurred (holes and protuberances). Too much randomness without governing rule dissolves the combs into protuberances and holes, and such a comb probably would not function well biologically.

After reviewing a great diversity of nests, Wenzel (1991) states, that the nest changes in a more or less predictable way as they grow and age, and variation is usually greater between old nests than between young ones. These assertion is supported both by our data on *Polistes dominulus*, and by our simulations. Both natural and simulated nests developed in a fashion matching a power function with a very high coefficient of determination. The dynamics of differential script did not differ significantly from the natural building in the natural range of this species.

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